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HUMAN RETINAL ADAPTATION

By Selig Hecht

Physiological Laboratory, College of Medicine, Creighton University, Omaha

Communicated by J. Loeb, January 2, 1920

Although the magnitude and the course of the dark adaptation of the human eye are well known, no fundamental interpretation has been made of the results. The data are simple. In the dark the eye becomes increasingly sensitive to light as the time goes on, until after about an hour it reaches a maximum of irritability. The measure of this changing sensitivity is given in terms of the least intensity which is just perceptible to the eye. The data which have been accumulated in this way are plentiful and accurate.[1]

The lack of theoretical significance of these data is caused by two conditions. The first is that the term sensitivity, even as measured in units of intensity, has no ultimate material basis. The fundamental question is: what objective changes in the makeup of the retina determine the variations in its sensitivity? This cannot at present be answered from experiments on the eye. However, even if this situation were satisfactorily elucidated, a second limitation bars the way to a final interpretation. This second condition hinges on the photochemical effect of the light. Since the data of retinal dark adaptation are given in terms of intensity, it is necessary to have some quantitative estimate of the photolytic action of light at the various intensities used for stimulation. This condition again cannot be fulfilled from the reported experiments with the eye. Indeed, in the present state of our knowledge it is difficult to devise experiments for the purpose of investigating these two conditions.

Fortunately the physicochemical analysis of the photoreception of lower forms has reached the point where these questions may be answered with considerable accuracy and a fair degree of confidence.[2] With regard to the first limitation of retinal interpretation, the experiments with *Mya* and *Ciona* are unequivocal. A photosensitive substance S is decomposed by the light into its two precursors P and A. This reaction is reversible, the regeneration of photosensitive material S from its two precursors P and A following the course of a bimolecular reaction. Thus the equation of the reaction is

$$S \underset{\text{“dark”}}{\overset{\text{light}}{\rightleftharpoons}} P + A.$$

The important point in this mechanism is that the sensitivity of the sense organ at any moment is dependent on the concentration of precursor substances P and A. Quantitatively expressed this means that the amount of fresh precursors that must be formed by the light before a response is elicited is always a constant fraction of the amount of precursors already present in the sense organ. Conversely, this amount of fresh precursors is a direct measure of the concentration of residual precursors. If this concentration is high, much fresh precursors are required, and much light energy must be used to produce the minimum stimulating effect. If the concentration of residual precursors is low, the reverse will be true. In short, the sensitivity is thus defined in terms depending on the physical constitution of the sense organ.

Similarly with the second condition which inhibits the interpretation of retinal adaptation. Experiments to be published in the *Journal of General Physiology* show a simple relation between the intensity of the stimulating light and its photochemical effect in the photosensory process. If E is the photolytic effect as measured in units of P and A formed, then the results are that

$$E = lnI$$

where I is the intensity of the stimulating light. The photochemical effect of the light is, therefore, a logarithmic function of its intensity. Here again the meaning of the minimum intensity is given in terms of the ultimate composition of the sensory mechanism.

If the initial phase of the photic reception of the human retina in dim light is similar to the mechanism in these lower forms, the application of the two principles just described should yield an analysis of the results obtained in dark adaptation. The sensitivity of the eye given in terms of the minimum intensity of the stimulating light can now be replaced by a direct statement of the photochemical effect of this light. Instead of the intensity we may use the logarithm of the intensity to indicate the extent of this photolytic activity. This now shows that during dark adaptation of the eye less and less photochemical decomposition is required to produce a visual effect. Assuming a photosensitive substance in the retina, this means that as the time goes on less and less of this photosensitive material must be decomposed in order to produce a stimulus. The exact amount of this decomposition can now be calculated.

If in addition it is true for the eye that the amount of freshly formed decomposition product is always a constant fraction of the residual decomposition product present in the retina, the significance of these facts becomes clear. During dark adaptation less and less fresh decomposition product must be formed. Therefore, the quantity of residual decomposition product present in the retina must also become less and less, and at the same rate as that of the fresh decomposition product. The ratio between the two being constant, the curve of dark adaptation should represent the rate of disappearance of the residual decomposition product.

The many experiments reported on the retinal adaptation of the eye, when analyzed in this way, show a uniformly consistent course for the disappearance of the decomposition product. The curve which represents all of the published data is the isotherm of a bimolecular reaction

$$k = \frac{1}{at} \cdot \frac{x}{a - x}$$

in which k has an average value of approximately 0.016. Because of the refined technic used in the experiments the agreement between the individual observations and the theoretical curve is frequently diagrammatic in its precision. An example is given in figure 1. The observations are taken from an experiment of Nagel's made more than ten years ago.

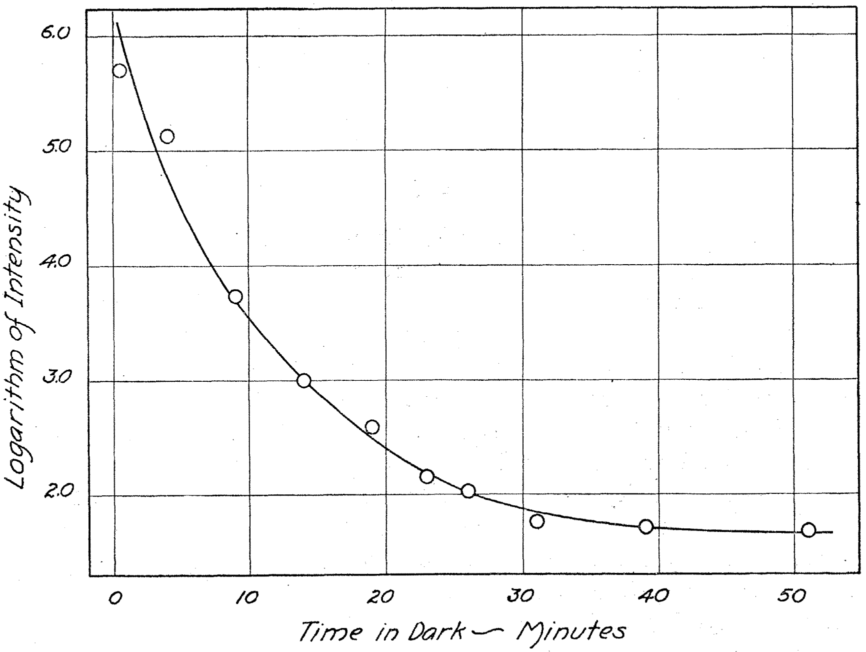

FIG. 1. Dark adaptation of the human eye. The points are single observations, whereas the curve is the isotherm of a bimolecular reaction. Actually the ordinates are the logarithms of the minimum intensities at different periods in the dark; theoretically they represent the number of units of decomposition products still present in the retina.

The meaning of the representation of the course of retinal dark adaptation by the curve of a bimolecular reaction is obvious. *Two* substances are decreasing in concentration according to the ordinary velocities of chemical reactions. These two substances are, therefore, combining to form a third substance.

The simplest interpretation of these facts is that the substance synthesized during dark adaptation is the photosensitive substance, and that the two materials which form this photosensitive substance are its precursors as well as its decomposition products. The initial process in visual reception in dim light must, therefore, depend on a reversible photochemical reaction in which a photosensitive substance is broken down into *two* decomposition products. During dark adaptation of the retina these two decomposition products then unite to form again the sensitive substance from which they were produced. The actual course of dark adaptation depends on the change in concentration of these two reacting substances.

In all essentials, then, the mechanism underlying the initial phase of retinal sensitivity in dim light is the same as that which forms the basis of the initial process of photoreception in such forms as *Mya* and *Ciona*.

[1] W. Nagel, in Helmholtz' *Handbuch der physiologischen Optik*, **2**, 1911.

[2] S. Hecht, *Journal of General Physiology*, **1** and **2**, 1918–20.

A KINEMATICAL INTERPRETATION OF ELECTROMAGNETISM

By LEIGH PAGE

SLOANE LABORATORY, YALE UNIVERSITY

Communicated by H. A. Bumstead. Read before the Academy, November 10, 1919

The concept of lines of force was introduced by Faraday as an aid in mapping out magnetic fields—these lines having everywhere the direction in which a small north pole would be urged by the field. Later it occurred to him that the characteristics of an electric field might be represented in similar manner by curves everywhere tangent to the electric intensity. Faraday limited his use of lines of force to static fields, and in cases where the field was produced by a number of charged particles, to the resultant field.

The electromagnetic theory of light, however, made it necessary to suppose that electric and magnetic lines of force in a wave front move with the velocity of light in a direction at right angles to their plane. Furthermore, the discovery of the electron made it natural to assume that when one of these small particles is in motion, its field is carried along with it. Wiechert and Stokes have explained X-rays as kinks in the lines of force emanating from such a particle—these kinks being propagated outward with the velocity of light whenever there is a change in the electron's state of motion.

The object of this paper is to show that the laws of electromagnetism may be explained exactly and in their entirety as kinematical relations between the moving elements which constitute lines of force, provided use is made of the space and time transformations of the principle of relativity in place of the more familiar but less philosophical Galilean transformations.[1] Each charged particle must be considered to have its own field, extending out to infinity in all directions, the resultant field at any point being a combination of those fields which extend to the point in question.